

Decomposition in tropical forests

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INTRODUCTION

It is a widely held belief that plant litter decomposes rapidly in the humid tropics, hence tropical rain forest soils have a low organic matter content and a major proportion of the ecosystem nutrient capital is located in plant biomass. The origins of these assumptions are obscure (Whitmore 1975) but are simply refuted by the widespread occurrence of podzols in tropical rain forests (Klinge 1966) in which more than 60% of the nitrogen and phosphorus capital may be located in the deep, organic humus-horizons of these soils (Klinge & Rodrigues 1968a, b). Nonetheless, the underlying dogma persists. Sanchez (1976), for example, presents extensive analytical data which show that temperate and tropical soils have similar organic matter contents, but he still concludes that 'in tropical rain forests neither temperature nor moisture limits decomposition at any time. These forests produce about five times as much biomass and soil organic matter as comparable temperate forests but the rate of organic matter decomposition is also about five times higher. Thus equilibrium organic matter contents are similar'.

It is the purpose of this paper to investigate the validity of generalizations regarding decomposition rates in tropical rain forests. We consider firstly the basis for comparisons of litter decomposition rates in different ecosystems and then attempt to interpret variations in decomposition rates at regional and local scales in terms of the regulatory variables of decomposition processes. We conclude by considering the importance of investigating decomposition processes for an understanding of forest dynamics, particularly when forests are cleared for agriculture.

COMPARATIVE MEASUREMENTS OF LITTER DECAY

The three most widely used measures of litter decomposition in terrestrial ecosystems are soil respiration, litterfall/standing crop quotients (k -values) and direct measurements of weight losses from litter bags. While these may continue to be the most convenient methods for comparative studies, each of them represents an over-simplification of the processes of decomposition and none of them provide true measurements of decay rates. The uncritical use of these methods may therefore hinder rather than assist our understanding of tropical decomposition processes.

Soil respiration is derived from respiration of the whole heterotroph community, mainly fungi and bacteria, plus the respiration of living roots. Root respiration is a very variable and poorly quantified component of soil respiration and estimates for the contribution of roots to total soil CO₂ efflux range between 21% at Pasoh in Malaysia (Ogawa 1978) and 67–82% for the root mat in an Amazonian forest at Manaus (Medina *et al.* 1980); a similar range of values has been recorded for temperate forests (Anderson 1973a). Thus, while soil respiration may be an indication of total carbon fluxes through the soil system (Schlesinger 1977) it is not a measure of carbon turnover by heterotrophic organisms or litter production. A comparison of soil respiration rates in tropical rain forests will not therefore be made (see Schlesinger 1977 and Medina *et al.* 1980 for reviews of the literature). Measurements of soil respiration, including root-free controls or methods such as those employed by Medina *et al.* (1980), can provide data on temporal and seasonal effects of temperature and moisture variation on heterotroph activity at different depths of the soil and litter profile. The importance of such measurements for an understanding of soil processes will become evident.

The relationship between litterfall and litter standing crops on the forest floor is widely used to compare litter decay rates or turnover times of forest floor materials. The use of these decay constants dates back to the classical studies by Jenny and co-workers in the 1940s, notably Jenny, Gessel & Bingham (1949), Greenland & Nye (1959) and the review by Olson (1963). Olson (1963) criticizes these earlier studies for their confusing differences in approach and proposes the use of the decomposition rate parameter '*k*' which is calculated as the litterfall divided by the soil organic matter standing crop under 'steady-state' conditions. Thus, tropical rain forests have *k*-values greater than 1, suggesting that the turnover of soil organic matter occurs in a year or less, while values of *k* for temperate forests are less than 1, and may be below 0.1 for coniferous forests, indicating turnover times ranging from a few years to several decades. Olson (1963) has, however, contributed further confusion by relating measured litter inputs to the soil system with total soil organic matter standing crops. It is rarely possible to calculate *k* values for total litter in terrestrial ecosystems, and not with the data set used by Olson, for three principal reasons. Firstly, living and dead roots are difficult to measure and differentiate and therefore have to be arbitrarily assigned to contribute to either input or organic matter standing crop. Secondly, large wood falls, particularly tree boles, are highly variable in space and time (at scales of hectares and decades) but make a significant contribution to soil organic matter standing crops. (For example, Yoda (1978) notes that deep humus layers were only observed at Pasoh where large fallen trunks had nearly decomposed.) Finally, the measured litterfall fractions are rarely divided into comparable fractions to the litter standing crop; in particular, the smaller particle sizes collected as 'leaf litter' are not generally defined.

Nevertheless, provided that the same litter components are represented in both inputs and standing crops the quotient, referred to below as the litter turnover coefficient *k_L*, represents the only basis on which geographical patterns of litter decay can be compared throughout the humid tropics with currently available data of very variable quality.

Finally, another widely used, short-term comparative measurement of litter decay is the loss of weight from material enclosed in mesh bags. Often different mesh sizes are used to exclude animals, or different size groups of animals, so that losses can be partitioned into the component processes of decomposition: microbial catabolism, the leaching of water-soluble materials and comminution through the feeding activities of animals. However, the separation of these processes and the measurement of weight or chemical composition of the residual material introduces a number of artefacts which make the results difficult to relate to other site measurements. These include different moisture regimes in the enclosed material to ambient conditions, the mesh size may exclude key faunal groups, animal/microbial interactions in decomposition cycling processes are altered or eliminated and the fate of material lost from the bags cannot be followed. This last point is of particular importance since fragmented or faecal material may be subject to totally different biotic and abiotic conditions to the parent material. The significance of this effect is considered below.

VARIATION IN LITTER DECOMPOSITION RATES

Data for litterfalls and litter standing crops in lowland rain forests and a few seasonal forests are given in Table 1 together with calculations of k_L for each site. Studies from lower montane rain forests and temperate deciduous forests are also given for comparison. The distribution of the data in Fig. 1 supports the proposition of Olson (1963) that litter turnover in tropical forests takes less than a year (i.e. $k > 1$). However, it is also clear that there is a substantial range in the rate of decomposition of both leaves and other components of small litter. Total small litter, which includes around 30–40% of woody materials, has a slower turnover rate than leaf litter but the relative differences between sites are generally consistent for these two types of litter resources of rather different composition. However, the extent of variation in lowland tropical forest decomposition rates (k_L values from 1.1 to 3.3 for small litter) is such that a number of sites are within the range exhibited by temperate deciduous forests (k_L from 0.4 to 1.4). Data for small litter turnover in montane forests show a closer similarity to k_L values for temperate forests than tropical lowland forests. Thus, the assumption that decomposition rates in tropical rain forests are always higher than in temperate zones is not borne out.

Comparisons of weight loss rates from leaves in litter bags can only be made in general terms since supporting data on decay rate determinants, particularly fauna populations, are generally lacking. This last parameter is important since mesh size influences access to different size groups of animals and the abundance of certain groups will determine rates of comminution.

Litter bag studies reported in the literature have been carried out over different time periods ranging from a few months to more than a year. For comparative purposes loss rates may be expressed as per cent per year, or per cent per day, assuming a linear pattern of weight losses although this is an over-simplification of the time-course of decomposition (Swift, Heal & Anderson 1979).

The results for litter-bag studies (Table 2) show that while the highest rates of

TABLE 1. Litterfalls, litter standing crops and turnover coefficients (k_L) for a range of tropical forests and temperate deciduous forests. Values are for total small litter* except where leaves are specified

| Study no. | Forest type and locality | Altitude (m) | | Litterfall (t ha ⁻¹ year ⁻¹) | Litter standing crop (t ha ⁻¹) | Turnover coefficient (k _L) | | Source |
|--------------------------------|----------------------------------|--------------|--------|---|--|--|--------------|------------------------------------|
| | | | | | | leaves | small litter | |
| Tropical lowland moist forests | | | | | | | | |
| (1) | Malaya, Pasoh Dipterocarp forest | 10 | | 10.6 | 3.2 | | 3.3 | Ogawa (1978), Yoda (1978) |
| | | | leaves | 6.3 | 1.7 | 3.6 | | |
| (2) | Ivory Coast | 50–100 | leaves | | | | | Bernhard (1970) |
| | Banco, plateau | | | 8.1 | 2.5 | 3.3 | | |
| | valley | | | 7.8 | 2.1 | 3.8 | | |
| | Yapo, plateau | | | 6.6 | 2.4 | 2.8 | | |
| | valley | | | 5.7 | 2.0 | 2.9 | | |
| (3) | Zaire | 300 | | 12.3 | 3.9 | | 3.2 | Laudelout & Meyer (1954) |
| (4) | Nigeria | | | | | | | Hopkins (1966) |
| | Evergreen forest | | leaves | 7.2 | 3.0 | 2.4 | | |
| | Seasonal forest | | leaves | 4.7 | 1.0 (wet season) 2.4 (dry season) | 2.8 | | |
| (5) | Nigeria | 250 | | 5.6 | 1.7 (wet season) 2.5 (dry season) | | 2.2 | Madge (1965) |
| (6) | Ghana, Kade | 150 | | 9.7 | 4.9 | | 2.0 | John (1973) |
| | | | leaves | 7.4 | 3.0 | 2.5 | | |
| (7) | Columbia | 30 | | 8.5 | 5.0 | | 1.7 | Jenny, Gessel & Bingham (1949) |
| (8) | Trinidad: <i>Mora</i> forest | | | | | | | Cornforth (1970) |
| | Vallencia | 40 | | 6.8 | 4.2 | | 1.6 | |
| | Matura | 200 | | 7.0 | 3.9 | | 1.8 | |
| (9) | Nigeria: bush fallow three sites | | | 7.0–9.7 | 6.9–11.7 | | 0.6–1.3 | Swift <i>et al.</i> (1981) |
| | | | leaves | 4.6–6.6 | 3.8–4.9 | 0.9–1.7 | | |
| (10) | Sarawak, Mulu | | | | | | | Anderson, Proctor & Vallack (1983) |
| | Alluvial forest | 50 | | 9.4 | 5.5 | | 1.7 | |
| | | | leaves | 6.6 | 3.8 | 1.8 | | |
| | Dipterocarp forest | 225 | | 7.7 | 5.9 | | 1.3 | |
| | | | leaves | 5.4 | 3.2 | 1.7 | | |

TABLE 1. (cont.)

| Study no. | Forest type and locality | Altitude (m) | Litterfall (t ha ⁻¹ year ⁻¹) | Litter standing crop (t ha ⁻¹) | Turnover coefficient (k _L) | | Source |
|-------------------------------|--------------------------|--------------|---|--|--|--------------|---|
| | | | | | leaves | small litter | |
| | Heath forest | 170 | 8.1 | 6.1 | | 1.3 | Anderson, Proctor & Vallack (1983) |
| | | | leaves 5.6 | 3.9 | 1.4 | | |
| | Forest over limestone | 300 | 10.4 | 7.1 | | 1.5 | |
| | | | leaves 7.3 | 4.2 | 1.7 | | |
| (11) | New Guinea | 100 | 9.8 | 8.2 | | 1.2 | M. J. Swift (unpubl.) |
| | | | leaves 7.3 | 5.0 | 1.5 | | |
| (12) | Panama, Barro Colorado | 150 | 13.3 | 11.2 | | 1.2 | I. N. Healey & M. J. Swift (unpub.) |
| | | | leaves 7.0 | 2.8 | 2.6 | | |
| (13) | Brazil, Manaus | 45 | 7.6 | 7.2 | | 1.1 | Klinge (1973) |
| | | | leaves 6.1 | 4.0 | 1.5 | | |
| (14) | Malaya, Penang | | | | | | Gong & Ong (1983) |
| | Dipterocarp forest | | 7.5 | 7.7 | | 1.0 | |
| | | | leaves 5.4 | 5.1 | 1.1 | | |
| Tropical montane rain forests | | | | | | | |
| (15) | Colombia | 1630 | 10.1 | 16.5 | | 0.6 | Jenny, Gessel & Bingham (1949) |
| (16) | Puerto Rica | 460 | leaves 4.8 | 5.1 | 0.9 | | Wiegert (1970) |
| (17) | Jamaica | 1550 | leaves 4.9-5.5 | 8.1-11.7 | 0.5-0.7 | | Tanner (1981) |
| (18) | New Guinea | 2450 | 6.8-7.6 | 6.1-7.7 | | 1.0-1.4 | Edwards (1977) |
| Temperate deciduous forests | | | | | | | |
| (19) | Holland | | 3.1 | 3.6 | | 0.9 | Witkamp & van der Drift (1961) |
| (20) | Belgium, Virelles | | 5.6, 5.3 | 5.6, 4.8 | | 1.0, 1.1 | Duvigneaud & Denaeyer De Smet (1970) |
| (21) | U.K., Meathop | | 5.4 | 7.1 | | 0.8 | J. Satchell in Swift <i>et al.</i> (1979) |
| | | | leaves 3.2 | 2.0 | 1.6 | | |
| (22) | U.S.A., Florida | | 10.7 | 8.2 | | 1.3 | Lugo, Gamble & Ewel (1978) |
| (23) | New Jersey | | 6.2 | 7.6 | | 0.8 | Lang & Forman (1978) |
| (24) | Missouri | | 3.5 | 6.1 | | 0.6 | Rochow (1975) |
| (25) | Tennessee: three sites | | 4.0-4.5 | 8.4-10.5 | | 0.4-0.5 | Harris, Goldstein & Henderson (1973) |
| (26) | Minnesota | | 4.6 | 12.6 | | 0.4 | Reiners & Reiners (1970) |

* Leaves, fruit, twigs and small branches (generally less than 2.5-5 cm diameter but unspecified in many studies).

weight losses (more than 200% year⁻¹) are greater than the fastest rates in temperate forests (less than 200% year⁻¹) there is considerable overlap between litter decomposition rates for the slowest tropical species and the fastest temperate species. Furthermore, although the rates of litter disappearance from coarse-mesh bags are generally higher than from fine-mesh bags this is not a particularly dominant feature of these results, suggesting that the impact of the macrofauna may not be as great as has previously been postulated (Swift *et al.* 1979).

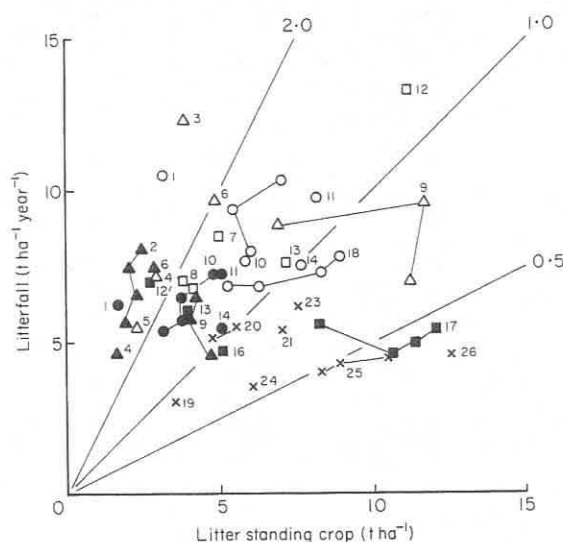


FIG. 1. Relationships between litterfall and litter standing crops in tropical rain forests of Africa (Δ), S.E. Asia and New Guinea (\circ), and the Neotropics (\square). Total small litter is shown as open symbols and leaf litter as solid symbols. Data for small litter in temperate deciduous forests (\times) are shown for comparison. The numbers beside the symbols refer to the data sets in Table 1. Lines have been drawn delimiting portions of the figure with litterfall/standing crop (k_L) quotients ranging from less than 0.5 to greater than 2.0. Studies carried out within a locality during a comparative programme of research are linked by lines.

The overall conclusion from this analysis of such limited data is that it is probably more important to seek the causes of variation in decomposition rates within the tropical forest biome than to seek for major differences between tropical and temperate forests.

DETERMINANTS OF LITTER DECAY RATES

Swift *et al.* (1979) suggested that decomposition processes are regulated by three groups of variables: the nature of the decomposer community (the animals and the micro-organisms, O), the characteristics of the organic matter which determine its degradability (resource quality, Q) and the physicochemical environment (P) which operates at macroclimatic and edaphic or micro scales. The decomposition rates of all materials are governed by these variables though their relative importance can vary

from site to site and resource to resource (leaves, wood, fruits, etc.). These variables interact but may be considered to have a hierarchical structure in the way that they influence one another in the decreasing rank order: macroclimate > microclimate > resource quality > organisms. Supporting information on these parameters is not

TABLE 2. Percentage weight losses from leaves in litter-bag studies carried out in tropical and temperate deciduous forests. Studies were carried out over widely differing periods of time and therefore results are expressed as % year⁻¹ for comparative purposes; thus, weight losses from rapidly decomposing leaves may exceed 100% over 1 year

| Site | Coarse mesh* | Medium and fine mesh† |
|---|--------------|-----------------------|
| Tropical lowland rain forests | | |
| Nigeria (Madge 1965) | 219-548 | |
| (Swift <i>et al.</i> 1981) bush fallow | 244-352 | 174 |
| Ivory Coast (Bernhard-Reversat 1972) | | 153-212 |
| Panama (Healey & Swift, unpubl.) | 150-352 | 120-183 |
| Sarawak (Anderson <i>et al.</i> 1983) | 52-61 | 53-65 |
| Amazon (Irmiler & Furch 1980) | 35-80 | |
| Tropical montane rain forests | | |
| New Guinea 2500 m (Edwards 1977) | 26-95 | |
| Jamaica 1400 m (Tanner 1981) | | 26-95 |
| Temperate deciduous forests | | |
| Belgium (Mommaerts-Billiet 1971) | 20-200 | |
| United Kingdom (Bocock & Gilbert 1957) | 34-186 | |
| (Bocock <i>et al.</i> 1960) | 37-96 | |
| (Anderson 1973b) | 26-58 (7 mm) | 27-50 |
| Canada, Quebec (Maldague 1967) | 66-77 | |
| Hungary (Toth, Papp & Lenkey 1975) | | 36-68 |
| U.S.A., New Hampshire (Gosz, Likens & Bormann 1973) | | 32-58 (3 mm) |
| Tennessee (Shanks & Olson 1961) | | 25-75 |
| New York (Woodwell & Marples 1968) | | 59 |
| Virginia (Orndoff & Lang 1981) | | 31-43 |
| New Brunswick (Strojan 1978) | | 37-39 |
| Minnesota (McBreyer & Cromack 1980) | | 29 (3 mm) |

* 10 mm or greater, unless stated.

† 2 mm or less, unless stated.

available for the majority of decomposition studies in temperate regions, let alone the tropics, and therefore we consider examples where a single factor appears to predominate in order to demonstrate its effects. In each section we attempt to explain how these factors may relate to the variations in decomposition rates demonstrated in the previous section.

Organisms

The decomposition of plant litter is brought about by a complex community of fungi, bacteria and invertebrate animals. The interactions within and between these groups

make the detailed processes of decomposition extremely difficult to investigate. At a gross level, however, the disappearance of intact litter from the forest floor is mainly a function of the nature and intensity of animal feeding activities; though this litter comminution is only a component process of decomposition (which also includes catabolism and leaching) and therefore cannot be equated with total litter decomposition (Swift *et al.* (1979). The macrofauna and some elements of the mesofauna (particularly termites) show some discrete patterns of distribution which can be related to rates of litter disappearance from the forest floor (Table 3) but for most of the

TABLE 3. Population densities (no. m⁻²) of saprotrophic macrofauna in rain forest sites, illustrating possible regional and local differences in the contribution of animals to litter comminution. Data are presented for four sites in Mulu National Park for comparison with the results of litter-bag studies given in Table 5. For details see text

| | Alluvial forest | Sarawak (Mulu)* | | Forest over limestone | Nigeria (Ibadan)† | Brazil (Manaus)‡ |
|--------------------|--------------------|-----------------------|-----------------|--------------------------|----------------------|---------------------|
| | | Dipterocarp forest | Heath forest | | | |
| Annelida | | | | | | |
| 'earthworms' | 42 | 26 | 24 | 6 | 34 | n.d. |
| Mollusca | | | | | | |
| Pulmonata | <1 | <1 | 0 | 6 | n.d. | n.d. |
| Crustacea | | | | | | |
| Isopoda | 26 | 17 | 20 | 40 | 415 | 27 |
| Decapoda | <1 | 0 | 0 | 0 | — | — |
| Myriapoda | | | | | | |
| Diplopoda | 17 | 3 | 21 | 71 | 1210 | 20 |
| Insecta | | | | | | |
| Blattodea | 9 | 8 | 10 | 8 | n.d. | 8 |
| Orthoptera | 6 | 4 | 8 | 17 | n.d. | <1 |
| Coleoptera | 46 | 63 | 35 | 15 | 260 | 279 |
| Isoptera | 254 | 1148 | 1408 | 50 | 30 | 1087 |
| Total | | | | | | |
| excluding Isoptera | 148 | 122 | 118 | 163 | 1919 | 335 |

Source: * Anderson *et al.* (1983);

† Madge (1965);

‡ Fittkau & Klinge (1973).

mesofauna, and most notably the microfauna (protozoa and nematodes), no such patterns have been shown. General considerations lead to the conclusion that, although varying in species composition, a microflora (fungi and bacteria) of comparable 'functional capacity' is probably resident at all sites and would not be a factor contributing to variation in litter decay rates. Thus, it is variation in the fauna and in *P* and *Q* acting on the microflora which determines variation in decay rates.

In temperate deciduous forests the role of earthworms in surface litter comminution, mainly associated with *Lumbricus terrestris* L., and pedogenesis is very variable and tends to be over-emphasized. There also appears to be an a priori expectation by temperate ecologists that tropical earthworms have equivalent roles in litter comminution, but there is little evidence that this is so. Firstly, none of the tropical earthworm

families are known to contain species which draw leaves down into the soil, as is a feature of temperate mull forest soils, and secondly the biomass of tropical earthworms is generally smaller than in temperate forests though their activity may be higher. The relatively low density and biomass of earthworms at Mulu (Sarawak) is similar to the populations ($0\text{--}44\text{ m}^{-2}$) and biomass ($0\text{--}0.2\text{ g m}^{-2}$) at Pasoh (Abe & Matsumoto 1979). These results may be compared to 250 m^{-2} (4.5 g m^{-2}) in a Nigerian forest (Madge 1965), 4.4 g m^{-2} in bush fallow and 2.5 g m^{-2} in cultivated Nigerian soil (Cook *et al.* 1980), $7\text{--}102\text{ m}^{-2}$ ($0.2\text{--}3.6\text{ g m}^{-2}$) in natural and cultivated soils in Uganda (Block & Banage 1968), and $100\text{--}400\text{ m}^{-2}$ ($3\text{--}6\text{ g m}^{-2}$) in humid Ivory Coast savanna (Lavelle 1975). Temperate deciduous forest on high base status soils frequently exceed 100 g m^{-2} biomass of earthworms but this is reduced to less than 10 g m^{-2} in acid forest soils (Edwards & Lofty 1977). The high surface casting rates of tropical earthworms (Madge (1965) records over $36\text{ t ha}^{-1}\text{ year}^{-1}$) may result in the burial of litter and a change in the environment in which decomposition takes place. There is, however, no current evidence of a central role for earthworms in surface litter decomposition in tropical rain forests although casts are known to be higher in carbon and mineral nutrients (Cook *et al.* 1980) than parent material. It is therefore probable that they are indirectly involved in enhancing microbial activity and nutrient fluxes.

The soil macrofauna of Mulu (Collins, Anderson & Vallack 1983) and Manaus (Fittkau & Klinge 1973) are similar in the low abundance and biomass of litter-feeding groups and again contrast markedly with temperate deciduous forests. The termite populations, however, are high in these two forests compared with other fauna but these figures mask the trophic roles of the groups involved. A major proportion of the Mulu populations are humus-feeding termites, which may have key roles in determining levels of available phosphorus in soils (Anderson & Wood, 1983), but do not attack intact litter resources. The litter-feeding Macrotermitinae are poorly represented in Mulu and are absent from the Neotropics. However, the abundance of Macrotermitinae is a notable difference between the Mulu and Pasoh forests.

Total termite populations at Pasoh were estimated at $3000\text{--}4000\text{ m}^{-2}$ ($2.2\text{--}2.6\text{ g m}^{-2}$) of which 60% were wood feeders, 25% soil feeders and 15% litter feeders. Wood and litter feeding *Macrotermes* species made up over 70% of the biomass and 32% of the daily litterfall was consumed by *Macrotermes carbonarius* (Matsumoto & Abe 1979). Lower litter standing crops were recorded in the vicinity of *M. carbonarius* mounds than elsewhere on the forest floor. The seasonal forests of Africa also have comparatively high populations of Macrotermitinae, while the evergreen forests contain more humus-feeders. Nye (1961) in Ghana and Hopkins (1966) in Nigeria both attributed a major role to termites in the disappearance of litter from the forest floor but neither the groups involved nor population densities were determined in these studies. The distribution and abundance of the Macrotermitinae thus appears to be an important determinant of decomposition pathways, particularly for wood. Collins (1981) describes an extreme situation where almost all the dead wood in Nigerian Guinea savanna was removed by these termites and little microbial decomposition took place *in situ*.

The low abundance of litter-feeding macrofauna in the Mulu sites has been noted

and weight losses showed no relationship to fauna populations: the highest litter weight loss rates from coarse-mesh bags were recorded in the heath forest, which has the lowest macrofauna populations, while the comparatively large populations of millipedes, woodlice and snails in the forest on limestone are not reflected by litter comminution rates. In fact, higher weight losses were recorded from fine-mesh than coarse-mesh bags on this site, possibly as a consequence of moister microclimatic conditions. It is probable that the absence of a general correlation between macrofaunal distribution and decomposition rates is due to the highly opportunistic and flexible nature of the decomposer food web. Whilst a particular group of animals, such as termites, may strongly and predominantly influence the pattern of decomposition processes, in their absence other groups of organisms, including the microflora, may show 'compensatory activity' so that the overall pattern of decomposition processes is not markedly affected. Consequently the current predictive value of faunal studies in relation to decomposition rates appears to be very low. This is emphasized by the paradox that rain forests generally appear to have lower soil fauna populations and biomass than temperate deciduous forests although tropical forest litterfalls, and nutrient inputs to the decomposer system, are several times higher than those of temperate forests.

Resource quality

The plant litter input to the decomposer community may be regarded as presenting a diverse range of resources of varying 'decomposability'. The resistance of a particular resource to decay may be related to one or more of a variety of intrinsic factors ('hardness', lignin content, nutrient content, plant secondary compounds, mass and particle size) which are embraced by the term resource quality (Swift *et al.* 1979). Thus, leaves in general are of higher resource quality and are decomposed more quickly than twigs and other woody materials. The components of resource quality act by regulating the activity of decomposer organisms and, as with environmental factors, variations in Q interact from site to site with variations in the organisms. For instance, wood which is a relatively intractable resource in one site may decay rapidly in another because of termite activities.

Resource quality therefore loosely accounts for variations in decomposition rate between different resources within the same or adjacent sites. For instance, I. N. Healey & M. J. Swift (unpubl. data) showed that for different leaf species in the forest at Barro Colorado Island, Panama, decomposition rates ranged between 150% and 352% year⁻¹ from coarse-mesh litter bags and 120% to 183% year⁻¹ from fine-mesh bags in the same site.

Resource quality attributes of mixed (freshly fallen) leaf litters in the four Mulu forests are shown in Table 4. Nitrogen, phosphorus, potassium and calcium show a general pattern of decreasing concentrations in the order: forest on limestone (LF) > alluvial forest (AF) > dipterocarp forest (DF) > heath forest (HF); though leaves from the limestone site have lower concentrations of potassium relative to the site rank order for other nutrients. Lignin and polyphenol concentrations show the opposite

TABLE 4. Leaf litter resource quality and disappearance rates of surface litter in four rain forest sites in Mulu National Park, Sarawak. Litter decomposition was estimated from weight losses of leaves in coarse- and fine-mesh litter bags and the turnover coefficient k_L was derived from litterfall/standing crop quotients. Soil organic matter standing crops (SOM) in the four sites are also shown. Data from Anderson, Proctor & Vallack (1983)

| Site | Mineral elements (%) | | | | Lignin (% dry wt) | Polyphenols (% tannin eq) | Litter bag wt loss at 1 year (%) | | Turnover coefficient (k_L) | | SOM* (t ha ⁻¹) |
|--------------------------|----------------------|------|-----|-----|----------------------|------------------------------|-------------------------------------|--------|-----------------------------------|-------|-------------------------------|
| | N | P | K | Ca | | | Fine | Coarse | leaves | total | |
| Lowland evergreen forest | | | | | | | | | | | |
| valley (alluvial) | 0.8 | 0.03 | 0.4 | 2.0 | 31.1 | 1.7 | 52.8 | 60.4 | 1.8 | 1.7 | 230 |
| ridge (dipterocarp) | 0.8 | 0.01 | 0.4 | 0.4 | 37.9 | 1.9 | 48.9 | 55.5 | 1.7 | 1.3 | 198 |
| Heath forest (kerangas) | 0.4 | 0.01 | 0.1 | 0.5 | 39.6 | 2.3 | 59.1 | 61.3 | 1.4 | 1.2 | 318 |
| Forest over limestone | 1.1 | 0.04 | 0.1 | 3.5 | 39.3 | 1.5 | 65.2 | 52.0 | 1.7 | 1.5 | 164 |

* 0–30 cm in AF, DF and HF; 0–11 cm in LF.

rank order to mineral nutrients for the three main sites, in common with resource quality attributes of most temperate forest litters, and the heath forest litter therefore has the lowest overall Q for saprotrophs. The leaves from the forest on limestone, however, have a high Q in all respects except the lignin concentrations which are similar to the heath forest. This unusual combination of high nutrient and high lignin concentrations makes it difficult to assess, *a priori*, the initial resource quality attributes of the limestone forest litter and emphasizes the need for basic research in this field.

In most respects the chemical composition of temperate and tropical forest leaves are very similar except for the high lignin concentrations recorded for the Mulu leaves (Anderson *et al.* 1983). There are few comparable data for tropical leaf litter but Singh (1969) reported lignin concentrations of 20–30% in a number of tree species from deciduous forests in India. High lignin concentrations may be a characteristic feature of long-lived leaves and, if so, it is likely that there are basic differences in litter resource quality between seasonal and evergreen forests.

There is no correlation between litter bag weight losses and resource quality for the four Mulu forest sites; in particular, the highest weight losses were recorded for the heath forest leaves which have the lowest Q . There is better agreement between Q and leaf litter k -values (which effectively integrate decay rates to the depth of the litter layer) but, while the highest soil organic matter standing crops occur in the heath forest, there is no correlation between Q and soil organic matter in the other sites.

Comprehensive data are available for mineral nutrient concentrations in tropical rain forest litter, particularly in leaves, but not for other resource quality attributes in the majority of decomposition studies. Reviews by Brasell, Unwin & Stocker (1980) and Proctor (1983) show that leaf litter nutrient concentrations range from 0.6 to 1.8% N, 0.02 to 0.44% P, 0.04 to 0.91% K, 0.2 to 3.0% Ca and 0.13 to 0.48% Mg. The leaf litters from Manaus, Mulu and Pasoh are towards the lower end of this range. In particular, the phosphorus concentrations in the Mulu leaf litters (0.01–0.04%) include much lower values than those at Manaus (0.03%) which were considered to be exceptionally low by Klinge & Rodrigues (1968a). The African forest litters appear to have higher nutrient concentrations, e.g. leaf litter from Kade, Ghana (Nye 1961) contained 1.9% N, 0.09% P and 1.0% K and showed higher rates of litter turnover than Mulu and Manaus. If percentage nitrogen is taken as an indication of litter resource quality there is a weak but significant overall correlation ($r = 0.49$, $P = 0.02$) between litter k -values and nitrogen concentrations in lowland forest litters from the main geographic regions (Africa: Laudelout & Meyer 1954; Nye 1961; Bernhard 1970. S.E. Asia: Proctor *et al.* 1983; Lim 1978. Neotropics: Klinge & Rodrigues 1968a; Cornforth 1970). Insufficient data are available for a more detailed analysis of relationships between Q and decomposition at this scale.

Climatic factors

The regulatory roles of physical environmental factors (mainly temperature and moisture) can be considered at climatic, edaphic (soil) or micro scales. In the latter case

the major effects are to induce local variations in the activities of decomposer organisms. This will not therefore greatly influence the major between-site differences shown in Fig. 1 but may account for some of the within-site or locality variation. It is therefore to the macro-scale, that of climate, that we address our discussion.

Meentemeyer (1978) has derived a function relating litter decomposition in temperate and tropical forests to actual evaporation (AE) and predicts that at an AE greater than $1500 \text{ mm year}^{-1}$ annual litter decay rates will be five times annual litter input to the forest floor. However, his data for the tropics are based on West African studies with particularly high litter decay rates and the function overestimates decay rates in most other tropical rain forests, other than Pasoh, by a factor of at least 2 or 3. In addition, Meentemeyer's values for AE, calculated by the Thornthwaite method, are closer to potential evapotranspiration (PE) or annual precipitation for the African sites than the values given by the M. I. Budyko complex equation in the UNESCO (1977) world maps of global water balances. We have attempted to relate litter k_L -values for rain forests to AE, PE and annual precipitation given in UNESCO (1977) but obtained no meaningful relationships let alone statistically significant correlations.

The particular problem with this approach is illustrated by the data for Manaus, Mulu, Penang and Pasoh (Table 1). Manaus and Mulu have similar k_L -values for leaves and small litter which are less than half those for Pasoh. However, Manaus and Pasoh have similar mildly seasonal climates with the mean annual rainfall around 2000 mm, while Mulu shows comparatively little seasonality with a mean annual rainfall exceeding 5000 mm. Finally, Penang has a similar climate to Pasoh but k_L -values which are less than a third of those for the other site. Clearly, at this scale, decomposition rates are not simply related to gross climatic variables and other factors are contributing to between-site variation.

However, the temporal effects of macroclimate on decomposition processes within forest sites are well documented for markedly seasonal forests where litter may accumulate during the dry season and decay rapidly during the wet season (Fig. 2). Some seasonality of litterfall and decomposition is a feature of most tropical forests but more information is needed about the balance of these processes at different times of the year. In many tropical forests peak litterfall occurs during the dry season but in Mulu maximum small litterfalls were associated with months of maximum rainfall (Proctor *et al.* 1983). The relationship between the onset of rain and the accumulation and decomposition of litter is a sensitive mechanism linking climate and the availability of plant nutrients. In Nigeria, Swift, Russel-Smith & Perfect (1981) found that during the dry season substantial amounts of P, N and other nutrients accumulated on the forest floor in the undecomposed leaf litter. Within 4 weeks of the onset of the rains all the accumulated P and half of the N was released through decomposition of the litter. By contrast, in the Mulu forests, these nutrients were immobilized in leaf litter and in most sites showed small losses of initial concentrations from litter bags after a year in the field (Anderson, Proctor & Vallack 1983). Wetting and drying events, both seasonal and temporal, are known to be important processes for carbon and nutrient mineralization (Swift *et al.* 1979). The flushing of savanna soils

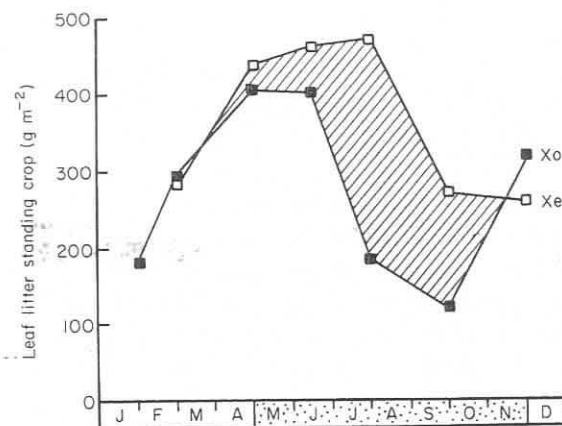


FIG. 2. The relationship of decomposition to climate. The observed change in standing crop of the leaf litter in the Panamanian forest during the year (X_0) is shown together with the theoretical line for the standing crop (X_e) if there was no decomposition, i.e. by addition of the monthly observed leaf litterfall to the initial standing crop for the month. The shaded area thus shows the estimated amount of leaf litter decomposed during each period between observations. Months with rainfall greater than 100 mm are shown stippled. Healey & Swift (unpubl.) in Swift *et al.* (1979).

was demonstrated several decades ago by Birch & Friend (1956), but we know of no detailed studies in rain forests.

PATTERNS AND PROCESSES OF DECOMPOSITION IN RAIN FORESTS

In general terms there is some evidence of regionality in litter turnover coefficients (k_L), with values greater than 2 for most African forests and between 1 and 2 for forests in S.E. Asia and the Neotropics, and the results of litter bag studies generally support this pattern. Both resource quality and particular groups of soil fauna appear to be contributory factors but gross climatic characteristics of the regions do not show the expected operation as the primary variable. Given the observed effects of seasonal climates on decomposition it is likely that an insufficiently sensitive expression of climate as a regulatory variable has been used, particularly in view of possible interactions with the variables of O and Q. We hypothesize that these interactive effects will include:

- (i) climatic determination of qualitative and quantitative characteristics of the decomposer fauna community;
- (ii) effects of seasonality on mineral and lignin concentrations in litter standing crop through variations in the timing of leaf-fall and the longevity of leaves;
- (iii) variations in the resource quality, quantity and location of root inputs under different climatic regimes;
- (iv) wetting and drying effects on carbon and nutrient mobilization and mineralization, particularly at the interchange between wet and dry seasons.

Meentemeyer (1978) has formulated a potentially useful approach to the interaction of these variables in a model linking decay rates to AE and lignin concentrations. His equation appears to have a good predictive value for temperate deciduous forests and for gradients in litter decomposition rates within the U.S.A., but underestimates leaf litter decomposition rates in Mulu by at least a factor of 2. We conclude that insufficient information is available at the present time to formulate realistic global models of decomposition. In particular, information is lacking on edaphic factors since both the litter bag studies and the litter turnover coefficients k_L bias interpretation of litter decomposition in tropical forests towards processes operating in the surface litter layers when the soil environment may be totally different at depth. Furthermore, the contribution of roots to soil organic matter must be taken into account.

A postulated effect of varying decomposition rates, implicit in the quotation from Sanchez (1976) cited above, is that there will be accompanying variations in the accumulation of soil organic matter. Thus, we may expect that if there is a high variation in decomposition rate then there will be reciprocal variations in the soil organic matter standing crops.

This relationship is explored in Fig. 3 where surface litter and soil organic matter standing crops have been plotted for forests located from the Equator to near the Arctic Circle. Surface litter standing crops show a wide range of values in most regions but there is evidence of a gradient in litter decomposition rates when it is considered that mean annual litter production varies from about 9.3 t ha^{-1} to 3.3 t ha^{-1} over the same latitudes (O'Neill & De Angelis 1981). Soil organic matter standing crops,

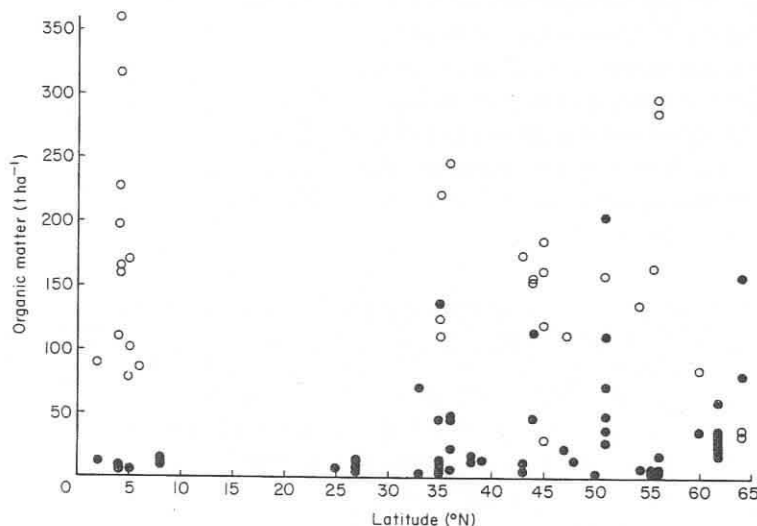


FIG. 3. Surface litter (●) and soil organic matter standing crops (○) in lowland forests ranging from equatorial regions to near the Arctic Circle. For comparative purposes tropical rain forest sites within 10° south of the Equator have been plotted at the same number of degrees north. Data from De Angelis, Gardner & Shugart (1981) and Proctor *et al.* (1983).

however, show no evidence of such a gradient and a wider range of values is shown for tropical rain forests than between tropical rain forests and the forests of temperate and boreal regions. Waterlogging can lead to the development of organic soils in the tropics (Mohr & van Baren 1954), particularly in montane forest (Whitmore & Burnham 1969; Grubb 1977; Tanner 1981), and the extensive lowland peat forests of west Malaysia are an extreme example of this phenomenon (Whitmore 1975). Other contributory factors to soil organic matter accumulation in tropical regions are the toxicity of aluminium ions to micro-organisms in acid soils and the complexing of humus materials with clays, particularly in volcanic soils containing allophane (Sanchez 1976). Edwards & Grubb (1977) noted high organic matter contents to considerable depths in the profiles of montane forest soils in New Guinea and suggested that stabilization by clay mineral complexing may be responsible.

The high organic matter contents of the four Mulu sites cannot be explained from available data, though Anderson *et al* (1983) suggest that waterlogging is a major factor in the heath forest podsol, and this serves to illustrate the necessity of integrated measurements of O, P and Q at different levels in the soil and litter profile in such studies. Interpretation of differences in the rates of nutrient fluxes through organic and mineral soil types, particularly in relation to the effects of disturbances, clearly depend upon a knowledge of the processes governing the accumulation of soil organic matter. Furthermore, decomposition studies are rarely carried out for sufficient periods of time for the effects of intractable fractions of the resources to be expressed. The experiments of Jenkinson & Ayanaba (1977) on litter decomposition rates in a cultivated Nigerian soil, using ^{14}C -labelled grass, are a good illustration of this effect. Decay rates showed a good fit to a double exponential model in which about 70% of the litter material decomposes with a half-life of 0.25 years and the remainder with a half-life of 8 years. In order to balance soil organic matter content, around 1% in the top 15 cm, with inputs it was necessary to postulate the existence of intractable fractions with a vastly greater half-life than those dominating losses over 2 years. In sites where comminution is a major component of weight losses on the soil surface the decomposition rate of faeces and litter fragments which settle into the humus layers may manifest this slow component of the decomposition time series and not the rapidly disintegrating experimental material in the litter layers.

EFFECTS OF DISTURBANCE ON DECOMPOSITION AND MINERAL CYCLING

The effects of disturbance on forest soil processes are manifested in changes in the regulatory variables operating at different scales ranging from very local events, such as tree-falls, the meso-scale of windthrow or patch cultivation to the large scale perturbation of clear felling for timber or modern agriculture.

Tree-falls

Tree falls are recognized as important local events for maintaining the mosaic structure of forest tree species but the regrowth of seedlings in these gaps has been often

interpreted in terms of the direct effects of changed light and moisture regimes. There are, however, also important indirect effects of the altered environment on plant growth through changes in decomposition and mineralization rates (Whitmore 1975). The opening of the canopy involves soil temperature changes as well as changes in the distribution and composition of precipitation compared with throughfall. Tree-falls also involve a large pulsed input of green leaves with high nutrient content and rapid decay potential. The effects of nutrients released under this combination of events can be related to the demonstration by Janos (1983), that the differential growth of seedlings is affected by the nature of mycorrhiza infections, to provide a testable hypothesis for a mechanism of forest tree replacement in gaps.

A tree-fall also deposits on the forest floor a massive bulk of nutrient-poor, highly lignified material in the form of stem and branch debris. The stumps and major roots of the tree also form a localized centre of low quality resources. The rate of decomposition of these materials may be very slow and, although Lang & Knight (1979) have claimed that tree boles may disappear within 10 years, the implication from studies of large woody litter turnover rates is that wood above about 3 cm diameter takes at least 15 years to decompose in tropical forests. Particular hardwood species may take much longer to decompose.

The significance of this is broad. The wood provides a source of energy for a wide range of micro-organisms and animals which may influence the general biology of the forest, and a physical habitat for many more. The resource is initially nutrient-poor but studies in temperate forests have shown that as decomposition proceeds it may become enriched by uptake of nutrients from ground and rainwater, and by import in colonizing animals (Swift, 1977; Ausmus 1977; Janzen 1976; Heal, Swift & Anderson 1982). Consequently, there may be a period in which the soil surrounding the fallen tree or stump becomes starved of nutrients as a result of immobilization by the wood decomposer community. Ultimately this package of nutrients will be released to enrich the surroundings. It is thus interesting to speculate whether the growth of seedlings and saplings within a tree gap is regulated by the nutrient uptake and release pattern of wood deposited in the area.

Cultivation

Clearance of forest and the preparation of land for cultivation involves more extreme environmental modifications. A study of field and fallow cultivation in Nigeria (Swift *et al.* 1981) showed that the temperature range at the surface of the soil was 18 °C in cultivated plots, compared with a diurnal variation of 3 °C within fallow forest plots, and the surface soil had a greater tendency to desiccate. The process of ploughing or hoeing alters the soil structure and the burial of litter results in extreme modifications of the material, physicochemical environment and the biota involved in decay. These changes result in an enhancement of litter decomposition in cleared areas of forest (Cunningham 1963; Swift *et al.* 1981) and accelerated nutrient release. However, Jenkinson & Ayanaba (1977) were unable to detect differences in carbon mineralization rates from ¹⁴C-labelled rye grass (*Lolium multiflorum* Lam. cv Westerwolth)

between open-field and forest-shade sites at I.I.T.A. in Nigeria. It is difficult to interpret the results of these experiments because soil temperatures were not measured in the sites and moisture conditions in the incubation tubes were also not determined. However, the overall decay rates in Nigeria, at mean annual soil temperatures of approximately 26 °C, were four times higher than in agricultural plots at Rothamsted (U.K.) at 9.2 °C.

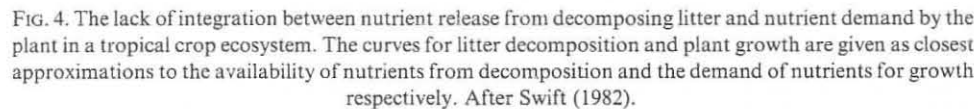
Information on the effects of agriculture on soil organisms is generally lacking but the importance of such studies for tropical systems is shown by the Nigerian project of Perfect, Cook & Swift (1980). The conversion of fallow rain forest to cow-pea (*Vigna unguiculata* L.) cultivation resulted initially in a dramatic decline in the abundance and diversity of all soil animal groups. After 2 years the numbers recovered but the community was considerably altered and with lower diversity. Similarly, whilst earthworm casting activity returned to levels comparable to those of the fallow, the dominant species was different. Maize was cultivated with and without DDT as an additional agricultural treatment before the plots were allowed to return to bush fallow. Crop production was lower in the pesticide treated plots and although soil nutrients were depleted by continuous cultivation there were no differences in the depletion from plots with higher yields. It was suggested that the more rapid decline in the fertility of the plots with a history of DDT treatment may be associated with pesticide effects on the soil biota (Perfect *et al.* 1979).

Termites are profoundly affected by forest clearance and cultivation. In Sarawak, Collins (1983) showed that in cleared forest there were six species compared with twenty-five in virgin forest and that the Macrotermitinae were less affected than other groups. In Nigeria four out of the original twenty-four species surviving after 14 years of cultivation were *Microtermes* (Macrotermitinae) which increased to over five times those in bush sites; most of the species lost were soil-feeding termites (Wood, Johnson & Ohiagu 1977). The role of soil-feeders in forest soils is unknown but their potential involvement in nutrient fluxes is indicated by the increased exchangeable cations and other nutrients after passage of soil through the termite gut. Concentrations of available phosphorus in mounds, constructed from faecal material, were up to seventy times those of the surrounding soil in a Nigerian forest (Anderson & Wood 1983).

One of the greatest changes in cleared and cultivated forest systems is in the qualitative and quantitative characteristics of litter inputs and has been recognized for some time as one potential feature leading to loss of soil fertility under cultivation (Nye & Greenland 1960). Factors other than the quantity of litter may profoundly affect the efficiency of nutrient return to the plant; but these are less well understood. In particular, the decrease in heterogeneity of litter constituents and the loss of synchrony between decomposition and plant growth should be emphasized since these factors can be manipulated by agricultural management.

The litter input from most arable crops lacks the lower resource quality components (woody resources in particular) that tend to stabilize nutrient cycling in forest ecosystems. The overall quality of agricultural litter may also be higher than the equivalent from natural ecosystems, because premature cutting of the crop may be carried out before nutrient withdrawal occurs. Thus, the major part of the litter will

The timing of litter input to the decomposers in agricultural systems is commonly dictated by management practices, particularly the cutting and ploughing-in of standing trash. The initiation of decomposition will commonly occur before seed planting and it is possible to predict that maximum nutrient release may occur *before* the crop is sufficiently established to benefit from the availability of nutrients (Fig. 4).



CONCLUSIONS

Decomposition processes can be investigated at many different scales of space, time and resources but at all levels the variables, O, P and Q, as defined, can be identified. The interaction of these variables in a mosaic of micro-sites determine the gross characteristics of decomposition for a particular forest site but a particular factor may locally dominate surface litter decay rates or soil organic matter accumulation. Thus, resource quality or the characteristics of the litter-feeding macrofauna can result in higher decay rates in temperate forests than tropical rain forests, or vice versa, which

conflict with the general assumptions about latitudinal gradients of decomposition rates.

Changes in the decay rate determinants, through tree-falls, or shifting cultivation or large-scale perturbations to the forest disrupt the integration between the plant and decomposition subsystems. At the small scale these disturbances are accommodated by ecosystem homeostatic processes, though there are implications for seedling regrowth in tree gaps, but the disruption of natural processes on larger scales requires urgent study. On one hand information is needed for soil conservation and forest management and on the other the decline in soil nutrient status and productivity one or two seasons after forest clearance is a feature of low intensity tropical agricultural systems. Temperate agriculture has bypassed the problem by using fertilizers or mixed farming. Alternative solutions are required for areas of the tropics employing planned manipulation of decomposition and nutrient release such as mulching, mixed cropping and other litter resource management techniques and these are being actively investigated in a number of research centres. The most urgent requirement is long-term studies into the effects of disturbance on soil biological processes in natural systems as a baseline for management.

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